XV. *The Evolution of the Habits of the larva of* Lycaena arion, *L.* By T. A. Chapman, M.D.

[Read October 4th, 1916.]

In presenting my observations on *L. arion* last year to the Entomological Society, I confined myself to the bionomics actually observed; nor had I thought out more than some very vague ideas as to how the remarkable habits of the larva had come about. A luminous comment by Mr. Bacot, however, made a starting-point for endeavouring to co-ordinate our knowledge towards its explanation. Like many such valuable suggestions it seems so simple and so probably true, that one feels sure that one surely had thought of it all the time. Yet I don't suppose that I or any one else had clearly done so till Mr. Bacot brought his trained acumen to bear on the point. Mr. Bacot's supposition is that " the doing away with moults after the entrance to the nest is a precaution against the temptation to the ants of a soft, newly-moulted larva." The initial point in the evolution of these habits would probably be that found in the case of those " blues " whose larvae are collected by the ants and placed on food-plants actually on the ants' nest, as occurs with *argyrognomon*, *coridon* and *bellargus* and probably other species. It may be a question whether the nest is not actually extended towards a suitable plant, but where this occurs plants and ants' nests are both numerous, so that their coincidence in locality is necessarily frequent. It might be said that the ants do take these larvae to their nests, as they leave them, when at rest, on the root stocks of their food-plants, and cover them with loose material; and I have seen ants remove a small larva that they appeared to think in danger when I disturbed them. A slightly deeper enclosure in the nest, and a cannibal proclivity on the part of the larva, would initiate the *arion* habit.

The normal number of moults in Lycaenines is four, and the normal instar for hibernation of those that hibernate as larvae is the third instar. I have not found any accurate record of these points in regard to the congeners of *arion* (*euphemus*, *arcas*, *alcon*), but, as they hibernate as half-grown larvae, the probability that they have the usual number of moults and hibernate in the third instar is very great. Nor, even should they deviate from this as regards one moult, as one or two Lycaenines occasionally do in one or other of these particulars, they equally form a base from which we may believe *arion* started in developing its extraordinary habits. In that case we may with considerable certainty assume that at first *arion* was carried into the nest in the third instar, and there hibernating initiated the remarkable indifference the ants show towards the larva, which would then be quite harmless, though they are now enemies that one would expect to be dreaded and combated.

It is probable that some of the larvae so carried in chose to take another moult before hibernating, as occurs in *A. pheretes* (Trans. Ent. Soc. 1912, p. 403), and, feeding in the interval, their cannibal tastes would enable them to get on by eating the larvae of the ant. Once this habit was acquired, further progress would in a sense be simpler, though there would remain the difficulty of two moults to be made in the ants' nest, and contentment with the diet of ant larvae in the spring to be acquired and fixed. If we assume an occasional variation in the instar for hibernation from the third to the fourth, accompanied frequently with an actual diminution of the size of the larva in these instars, we make a further step. It is very likely that the variation in the instar of hibernation from the third to the fourth is really due to some privation of the larva, that made it badly grown and nourished in the third instar and ill-equipped for hibernation. My experiments on the larvae of *Agrotis comes** and others showed that starvation often led to an extra moult; here, of course, the moult is not an extra one, but an antedating that would be of similar effect.

These larvae in the fourth instar would not be much larger than the usual third-stage larva, and would be equally within the power of the ants to carry. We do not know whether the ants would prefer a larger or smaller larva, but probably the latter, as that has been the direction in which *arion* has varied. A tendency to vary towards diminished size would also be involved in the causes leading to hibernation in the fourth instar. As to losing the fourth moult, this would present few difficulties, the most parallel case I know of being that of *Acronycta alni*, which has lost a moult as compared with its nearest relatives. The loss is associated with the remarkable change from the bird-dirt-like young larva to the handsome and conspicuous last-stage one. Now and then an individual resumes the lost instar and presents a stage intermediate between the two forms—obviously a form that is neither flesh nor fowl and therefore has been lost, but not so completely as not to reappear sporadically. *Moma orion* presents in each brood a larger and a smaller race, the former with one more moult.* *O. antiqua* and many other species present examples showing that the losing or gaining of a moult is not an infrequent occurrence. *Orgyia antiqua* has, in fact, in each brood two races—one with a moult less than the other, and each with a moult less in the male than in the female; this is probably correlative, along with the long period over which the eggs of one brood go on hatching, with the fact that this single-brooded (in England) species is on the wing from early summer till late autumn, fresh specimens emerging during several months.† To return to *L. arion*.

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* E. M. M., vol. xxxii (1896), pp. 54, 80.

We may admit that whilst still plant-feeders they were less cannibalistic than now; but, as it is a characteristic not infrequent in other blues, they would take not unreadily to eating ant larvae, and we may assume that a certain percentage survived the difficulties of a purely animal diet (*Calymnia trapezina*, e. g., can be reared on oak (or other) leaves, or entirely on other larvae), and the dangers from the ants, which would be greater just after moults. If so much be granted, and it seems all very simple and straightforward, the advantages of protection during the winter and an assured dietary would largely balance the disadvantages and dangers. These would be eliminated as certain larvae dropped a moult and were accordingly at an advantage, and assuming as possible they were first carried in in the third instar, a diminution in size at moults would lead to a change to fourth instar for the translation. This diminution in size would be favoured, if the carnivorous habit was advantageous from a nutritive aspect; since the larvae that grew least on thyme and so got earlier into the

* Ent. Record, vol. iii, p. 220.

† E. M. M., vol. xxiii, p. 224.

nests would benefit, and also the ants would more easily transfer them.

The assumptions here made are not very far-fetched, and if they be granted it becomes possible to understand how such a remarkable life-history became evolved. It is to be remembered that this history refers only to *L. arion* (probably also to *arionides*, which though a distinct species is exceedingly close to *arion*), and that its congeners (*euphemus*, *arcas*, *alcon*) have ordinary Lycaenine life-histories, so that the evolution is comparatively modern and does not involve an ancestry including other species, and therefore does not imply a number of conditions probably unknown to us. That is to say, there can be no doubt that *L. arion* itself developed these curious habits, and did not inherit them from any other species with ant-hosts. To settle certain points that at present we can only guess, it is necessary to know the precise life-histories of the congeners of *L. arion*, especially how many moults they have, and in what instar they do hibernate. Though all those larvae are known, I cannot find definite records on these points. I have reared *melanops* and *cyllarus* and have had the early larva of *L. alcon*, when it mined in the tissues of *Gentiana pneumonanthes*, but I carried it no further; it is, however, well known that *euphemus*, *arcas*, and *alcon*, which are certainly congeneric with *arion*, pass the winter as partly-grown larvae, presumably in the normal third instar.

Cyllarus and *melanops* are not congeneric with *arion*, and both, I think, pass the winter as pupae.

We want actual observation of how the ants collect to one food-plant on the nest the larvae of *coridon*, *thetis*, *argyrognomon* (these, I feel sure, *are* so collected), and probably others. This habit might easily merge into one of carrying the larva into the nest. In the three species I have mentioned the cannibal habit hardly exists, so that a larva in the nest would almost certainly perish of starvation, and thus no *arion* habit would be initiated. Perhaps the most remarkable fact as regards the hibernation of *L. arion* is that it does so as a half-grown larva in the last instar. No other Lycaenid is known to do so. This change of habit must have developed after the use of the ants as hosts was established, and is perhaps the most difficult fact in the life-history of which to suggest the development.

In discussing various of those matters later with Mr. Bacot, he makes certain comments that may lead us further; but, at any rate, a short note of them may clear up some points and present others as yet insoluble. Were the larvae not *always* carried in in last instar? This seems very improbable, as the only larvae of Lycaenines that hibernate in last instar do so when full-fed. The carrying in would be done probably in third instar, and at the same time and at any rate later, but at first much more rarely, in fourth instar, but previous to a fourth moult. The ants would be likely to attack a larva when soft just after moult, but probably did so rather infrequently, but sufficiently often to make the dropping of the fourth moult advantageous. All this, however, may be incorrect, and the actual adaptation more easy, if it be the case that *Lycaena* (as now represented by *euphemus*, etc.) only moult three times, and so forth.

How does *Liphyra brassolis* manage its moults? It is clearly regarded by the ants inimically, and has a suit of very strong armour-plate.

Would the ants not select the smaller larva, first of third instar, and, as the selection diminished the size of the larvae in each instar, then of fourth instar?

In view of the comparatively gigantic larvae of *argyrognomon* I have seen ants carrying, viz. small in last instar, it seems more probable that the ants took larvae of any size, since fourth-instar hibernating larvae would not be too large for them, and that the diminution in size was the result of an effort to reach as early as possible the more nutritive food afforded by the ant larvae, *i. e.* of course that larvae that were sooner in such better circumstances had a survival advantage. Mr. Bacot asks is there anything known of the danger from ants to the external feeding species at the period of the moult, or, a parallel question, is there any suggestion of a specially quick rehabilitation of the honey-gland in contradistinction to other details after a moult? So far as I can say I think the answer is that we know nothing on these points. The larvae I have found on plants on ants' nests have been in various instars, so probably quite escape attacks at moulting; but this is only guessing. The ants also build tents over individual larvae, and obviously regard them as valuable cattle to be carefully tended and defended, but they *may* eat a tempting larva nevertheless, but I feel tolerably sure that they do not. It is also the case that the larvae leave these tents to feed, and return to hide themselves in the ground amongst the debris covering the ants' nest—a habit that obtains even if the soil beneath the plant has no ants' nest in it, as they nevertheless hide in the soil by day if they can get under it, or if they cannot penetrate it, then amongst the plant stems close to the ground. It is therefore possible to say that the larvae protect themselves in this way during moulting.

I feel interested in all this as mere speculation, for others I may submit that its value consists in showing that whilst we have solved some important and interesting problems in the life-history of *L. arion*, we have opened the view of others that will require probably even more careful work and prolonged observation and experiment to solve them.

(October 2.) Since writing the above, I have received from Mr. Harold Powell some material bearing on the life-history of *L. alcon*. The mature larva described as green, etc., lives, according to report, on *Gentiana pneumonanthe* in spring, and I have already referred to its first stage. Mr. Powell found the food-plant bearing many eggs; when he came to examine them, however, he discovered the curious circumstance that they were all empty, the larva escaping from the lower aspect of the egg, leaving it looking intact and apparently full—a circumstance that only occurs in any Lycaenine, whose eggs I have had, as a really rare accident. The young larvae, however, had not bored directly into the plant tissues beneath, but had apparently entered the flowers.

Mr. Harold Powell, however, sent me heads of *Gentiana pneumonanthe* (Sept. 22, 1916) in the flowers of which larvae of *L. alcon* had fed; unfortunately they had practically all left the flowers for some unknown place (for hibernation). An examination of the flowers showed, however, abundance of eggshells, generally laid on the calyx, from which the larvae had escaped from the under surface, entering the still unopened flower. A close search was rewarded by cast heads of the first instar, and one dead larva in this instar. Skins cast at the second moult were abundant, *i. e.* there were usually several, often four or five, in one flower. One dead larva was found, just about to moult for the third time; inside the skin was the rather immature fourth-instar larva.

It may be that all the larvae reach the fourth instar (like *arion*) before hibernation; but since all the third-instar larvae had gone, presumably to hibernate, and only this one taking another moult was left, I take it to have been an exceptional individual taking an additional moult (as occurs in *pheretes*). So exceptional, however, as to be usually a failure, as in this case. Such a variation occurring in (the original) *arion* would obviously facilitate the acquisition of its peculiarities as regards moulting. Of course *L. alcon may* have the same habits as *L. arion*; we do not certainly know, but the mature larva is known and has a green coloration, like most of our other Lycaenids. The swampy places where *G. pneumonanthe* grows are not suitable for abundant ants' nests, and they would have to be abundant, as the butterfly swarms in the locality whence Mr. Powell sent me the flowers, and many flower-heads had a large number of eggs on them, probably each laid separately; the larva has a well-developed honey-gland. The flower-feeding larvae of *L. arion* are fiercely cannibalistic; the numbers of *L. alcon* that live amicably together in the same flower show that it is entirely free from such a habit.

If *arion*, then, like *L. alcon*, occasionally entered the fourth instar before hibernating, the question as to moults resolves itself merely into losing the fourth moult; but not really quite so simply as this, since the fact is not so much the loss of a moult as the loss of an instar, viz. the fourth, the third moult not resulting in a penultimate, but in the last instar. This is the fact in *Acronycta alni*, and should be as easily obtained in *L. arion*.